# Genetic Advances Among Pines of the Northeast

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ABSTRACT:-- A large proportion of forest genetics research in northeastern U.S. has been concerned with pines. Extensive provenance tests of *Pinus strobus* have provided useful information about genetic variation among and within populations in growth rate, winter injury, flowering, chemical constituents, and other traits. Much of the research has been aimed at developing varieties with improved resistance to white pine weevil and white pine blister rust. Research on *Pinus rigida* has been directed mainly at developing hybrids with *P. taeda.* Referred to as "loblollies for the North", these hybrids from carefully selected parents appear to combine rapid growth with adaptation to cold winters and poor sites. One problem which needs to be solved is how best to produce hybrids in commercial quantities. In *Pinus sylvestris* genetic variation of many traits and racial hybridization have been studied more extensively than in any other species. Christmas tree growers in the Northeast have been eager to apply research results in obtain ing seed from better provenances, but have been reluctant to invest in long term selection and breeding programs. Seed orchards have been established with these three pines and several others, but progeny testing and advanced generation breeding have been quite limited. Relationships between tree improvement and forest industries are discussed in evaluating accomplishments and future prospects.

## INTRODUCTION

Pines have been in the forefront of forest genetics research in northeastern United States. Over one-third of the articles dealing with particular species in Proceedings of the Northeastern Forest Tree Improvement Conference (NEFTIC) have been written about pines. The index for NEFTIC Volumes 1 to 20 lists 52 pine species and 43 hybrids. Eastern white pine accounted for nearly half of the articles, and Scotch pine another fifth. This high frequency of papers on pines probably is typical also of scientific journals, experiment station reports, and other publications.

The extensive research by many investigators on pines of the Northeast obviously cannot be covered adequately in one brief paper. Therefore, my review is limited to three examples selected for their scientific and practical significance: eastern white pine, pitch pine - loblolly pine hybrids, and Scotch pine. These species also occur outside the Northeast, of course, and so does research on them; thus the topic is consistent with the cosmopolitan spirit of NEFTIC, and I have not felt overly constrained by geographic boundaries.

My intent is to review some of the most significant research results, and how they relate to practical genetic improvements in the selected species. My comments are based on representative literature (not exhaustively documented), and on personal impressions I have gained during the past 25 years.

## EASTERN WHITE PINE

The preponderance of genetic research on eastern white pine, compared to other pines of the Northeast, can be justified by sound reasons. Because of its fine wood quality and abundance, white pine dominated the lumber industry for 250 years, from colonial times into the industrial revolution. Its uses over the years included everything from shipmasts to matches, clear and knotty-pine lumber, ornamentals and Christmas trees. The potential for rapid growth and good form on a wide range of sites have made it a favorite for reforestation in the Northeast, the Lake States, and several other parts of the world. In second-growth stands, however, tree quality commonly has been inferior, especially where white pine weevil or blister rust have been prevalent. Some lumbermen in New England are increasingly concerned about the declining quantity and quality of white pine timber.

Our knowledge about genetic variation in white pine has progressed in 25 years from meager evidence that some populations differed (Pauley et al. 1955) to range-wide information about many traits derived from numerous test plantings. Large provenance experiments carried out with assistance from many cooperators were organized first in 1956 by the U.S. Forest Service, and later through Michigan State University, USDA Regional Research Project NC-51, and the University of Maryland (Funk 1979, Garrett et *al.* 1973, Genys et al. 1978, Wright 1970 and 1976, Wright et al. 1979). These have provided very useful information about population differences in survival after planting, growth rates, winter injury, flowering, and chemical constituents. When grown in states from lower Michigan and Pennsylvania southward, certain populations had up to 70% greater height (Wright 1976) and five to eight times the volume (Funk 1979), compared to slow-growing populations. In more northern plantations differences have also been significant but smaller, and different populations have performed best in various locales. Faster growth has not resulted in lower wood density. Populations from the southern Appalachian mountains characteristically exhibited faster growth, but were injured by cold winters in northern plantations. Despite some consistent trends, genotype-environment interactions caused different populations to be the most desirable for various locations. Therefore, seed source recommendations must be specific for planting regions.

Considerable genetic variation among stands and within populations also may be exploited. (Kriebel *et al.* 1972, Sprackling and Read 1976, Wright 1976). Selection of the best provenances and parent trees sometimes is not a simple matter, as results of Sprackling and Read illustrate. In a test of 21 southern provenances, the tallest and shortest came from stands only 25 miles apart. Among 10 parents of the tallest population, the next to slowest-growing parent tree produced the tallest progeny, while progeny of the fastest-growing parent ranked eighth. Such results emphasize the difficulty of phenotypic selection in forests and the importance of testing provenances and progenies at several locations.

Improvements in disease and insect resistance of white pine would be especially valuable, and thus have received much attention in research. Most of the work on blister rust resistance has been conducted in the Lake States and Ontario, where the disease has caused more extensive damage (Bingham et al. 1972, Patton and Riker 1966). White pine weevil is the more serious pest in many parts of the range. Various kinds of studies have been directed toward improved weevil resistance, often with ambiguous and discouraging results (Brigden et al. 1979, Connola and Wixson 1963, Garrett 1972, Gerhold 1972, Gerhold and Plank 1970, Heimburger and Sullivan 1972, Santamour 1965, Soles 1970, Soles et al. 1970, Stroh and Gerhold 1965, Van Buijtenen and Santamour 1972, Santamour and Zinkel 1977, Wilkinson 1979 a and b, 1980). Only limited progress has been made in relating anatomical bark characteristics, oleoresins, or resin crystallization to resistance. Techniques have been developed using caged weevils to select seedlings or older trees for resistance to feeding and oviposition (Connola and Beinkafner 1976, Gerhold and Soles 1967, Plank and Gerhold 1965, Soles and Gerhold 1968) or using direct measures of weeviling in plantations (Wright and Gabriel 1959), but these have not been used in any program of selection and breeding. The most promising short-term solution remains one suggested by Wright and Gabriel (1959) over 20 years ago, i.e. to interplant the proven weevil-resistant western white pine with eastern white pine in areas where blister rust is not a serious threat. Western and eastern white pine hybrids also should be investigated. Wilkinson (1980 Mg) is pursuing these possibilities, and has new evidence supporting their merit.

Eastern white pine seed orchards have been established in several states. Most of the grafted clones were selected in natural stands according to different criteria, mainly concentrating on size, form, and branching habit. Progeny testing has been either limited or absent, and thus most clones have promise but not proof of genetic superiority. Although the seed orchards represent sizable improvement efforts, there is at present no comprehensive breeding program resembling those of the southern pines.

In considering how much of the genetic research with white pine has been applied in the Northeast, I must conclude that it is quite a small proportion. Presumably some of the provenance information has been utilized in purchasing seeds for nurseries and in making selections for seed orchards, but probably not very much. Seed orchards are producing only limited quantities of seeds, generally of unproven superiority, and it is not known if these will result in any improvements in forests due to lack of testing. White pine improvement programs generally are small, lack continuity, and are not likely to achieve any improvements in weevil resistance or blister rust resistance in the near future, unless they become better coordinated and focused on clearer objectives.

## PITCH PINE

The outlook for improvement in pitch pine is brighter, though until recently it was a dark horse in the tree improvement race. Pitch pine was not even mentioned in NEFTIC Porceedings until the 10th conference, when Mergen and Stairs (1963) reported on its use as a guinea pig in studies of gamma radiation. The species has a reputation for slow growth and crooked form, especially on poor sties (Ledig and Fryer 1974). A literature review in 1969 by Fryer and Ledig (1971) questioned "Whether pitch pine will ever prove to be of value to tree improvement in its own right." However, they did take note of the beginnings of tree improvement in 1963 (Little 1965), and the phenomenal hybridization program of Hyun in Korea.

Just one decade later, the prospects for pitch pine had improved dramatically. A range-wide provenance experiment had been started by Ledig and co-workers (1976). Little and Trew (1976, 1977, 1979) had the vision to realize the possibilities of pitch pine - loblolly pine hybrids, and the tenacity to carry their program forward though they encountered initial skepticism and difficulties in securing support. Having demonstrated the superiority of some of these pine hybrids at 29 test plantings in nine states, they now audaciously refer to them as "loblollies for the North?" The objective of this program from its inception has been to produce winter-hardy, fast-growing yellow pines adapted to a wide range of sites in the Northeast. Industrial support and direct participation undoubtedly are among the reasons for success achieved so far.

Preparation for hybridization began with the selection of 32 pitch pines phenotypically superior in height and form in eight states, from Virginia to Maine; and 33 loblolly pines native to Maryland and Delaware. These were grafted into a breeding orchard in New Jersey, where during seven seasons over 2400 pollination bags were mounted, most of them on the more precociously flowering pitch pines. All matings were between two clones. Because of loblolly pine pollen shortages, selected trees in South Carolina and Virginia also were used as male parents.

Height and survival data have been reported for eight olddr plantings in six states. The best of the hybrid families consistently outgrew the loblolly pine check from Maryland, the pitch pine check from the breeding orchard, and a hybrid Korean seedlot derived from unknown provenances. At various locations the best families were different ones, due at least partly to the fact that the families were not planted at all sites. The possible existence of genotype-environment interactions cannot be determined from reported data. There are indications that the extensive, fibrous root systems may enhance the adaptation of hybrids to droughty sites. They also grow well on northern loblolly pine sites, and are damaged less by winter injury, ice, and snow. Growth is generally slower in northern plantations, but the northern limits have not yet been determined.

Some serious questions must now be faced concerning future directions of this program. Perhaps the most crucial one is how to mass-produce the hybrids. Finding a solution requires comparisons of the merits of $F_1$, $F_2$, and backcross hybrids, and exploring the operational feasibility of vegetative propagation, artificial application of pollen, or other schemes for designing and managing seed orchards. Further testing will also be needed to determine which parent trees are best, and to which sites various kinds of hybrids are best adapted.

## SCOTCH PINE

In the search for a better brand of Scotch pine, there are similarities with the work on white pine and pitch pine, including extensive provenance testing and some hybridization studies. The widespread interest in growing and improving Scotch pine has been fostered by traditions in European forestry, and by the ease of growing this pine on a broad range of sites at middle latitudes across North America. Its principal use here is for Christmas trees, which is definitely not in the European tradition. Plantations generally exhibit very good survival and rapid initial growth, compared to most other northern conifers. Yellowing of foliage in winter, crooked stem form, and declining growth after trees reach pole size are the chief reasons why Christmas tree growers and foresters have become disillusioned with the species. Much better results have been achieved by matching selected seed sources with appropriate sites.,

Nurserymen and tree growers were well aware of variation in several traits associated with seed sources before geneticists published results of contemporary provenance tests (e.g. Bramble and Cope 1947). The first comprehensive reports from the Northeast became available after 1955 (Baldwin 1956, Wright and Baldwin 1957). These early experiments did not include any of the southern provenances that were later found to have much better color. Schreiner (1956), having conducted a reconnaissance of the species in Spain in May 1955, reported that native trees had excellent color and stem form. In 1954, W. C. Bramble at Penn State was already growing experimental seedlots he had imported from central Spain, having read about these "permanently bluish-green plants" in a publication from Sweden (Langlet 1936). Commercial nurserymen started growing Scotch pine from Spain soon afterwards, before test plantings had been evaluated. This illustrates the eagernerss of Christmas tree growers to exploit potential genetic gains. By 1963, when more definitive information started to become available from studies by Wright and his collaborators (e.g., Genys 1976, King 1965 a and b, Ruby and Wright 1976, Wright and Bull 1963, Wright et al. 1966) many growers already had trees from southern France, Spain, and Turkey in their plantations.

An entire chapter in Wright's text (1976), "Introduction to Forest Genetics," is devoted to a summary of genetic variation among Scotch pine provenances. This chapter that at first may seem impressive in length is in fact a greatly condensed and abridged version of the thousands of pages written on this subject, as no other species has been studied so extensively in so many characteristics. The wealth of knowledge about variation in growth rate, foliage color, stem form, branching habit, winter hardiness, disease resistance, insect resistance, and other traits of Scotch pine cannot be adequately distilled here. I do want to note that this information has been widely used in seed purchases by the Christmas tree industry, including many documented superior genotypes. These may be utilized for further research, selection, and breeding. The limited extent of genetic applications has been disappointing, however, in pines and also other trees of the Northeast.

Why has genetic progress been so much greater in the South than in the Northeast? Let me attempt an explanation by way of an analogy: tree improvement may be thought of as sailing across a sea of genotypes, in quest of an improved variety somewhere over the horizon. The early work with southern pines could be compared to the voyage of Columbus. This bold, clever explorer knew in what general direction to proceed, and sold the idea of glorious rewards to his sponsors. But he carefully avoided exaggerated claims of genetic gains, knowing that he had to sail through uncharted seas of genetic variation, and that the day of reckoning with his sponsors lay ahead. His sails, held aloft by the masts, spars, rigging, and hull of the improvement program's operational plans, were set to catch the shifting winds of financial support which impelled him onward. The keel of genetic theory enabled the helmsman to keep on course, steering with the rudder of a rudimentary selection method to make steady headway toward the goal of an improved variety. The skipper, constantly alert for wind shifts or threatening shoals, directed his helmsman and crew to make changes in the course or the set of the sails, tacking to adjust to economic vagaries and new knowledge of genetic variation. The first landfall was not the destination Columbus had expected. But he returned with treasure for his sponsor, nevertheless, and with tales of greater accomplishments to be had from future voyages. His success was dependent upon a combination of ingredients: a vision of a well-defined goal, an understanding of the realities of nature, the capabilities of ships and crew, and securing adequate support for the venture.

The fleet of smaller sailboats plying the northern pine seas has not been as well endowed or as well organized. Limited in size and range, they have taken short voyages in many directions, improving their sailing techniques and charting genetic variation as they progressed. Some encountered tricky currents and shifty winds of support, and thus had to change course frequently. Others were becalmed, struck reefs, or were simply abandoned to the forces of nature. Experienced skippers, through superb seamanship, have made their way to intermediate destinations, but their cargoes have not been in great demand. Some potential sponsors have withheld support, waiting to learn the fate of Columbus. Most have been dubious of the treasures waiting to be discovered, but some are showing signs of taking a plunge.

This nautical, analogy has been afloat long enough to serve its purpose. To avoid any further risk of mal de mer, let me return to terra firma fora more explicit summary.

The diverse and changeable management objectives of numerous, small owners of floristically diverse forests in the Northeast have made intensive silvlcultural practices the exception rather than the rule. Accordingly, incentives for long term investments in tree improvement have been relatively weak. Numbers of trees planted per species are much smaller than for loblolly pine, and therefore the prospective returns from genetic investments are more limited. Until recently, there has been little concern about possible shortages of raw material for pulp mills and sawmills, and natural regeneration of cutover forests usually has been satisfactory, if not optimum. So industrial forest owners have been more accustomed to harvesting timber than to planting and growing trees. These are the principal reasons why tree improvement has progressed more slowly in the Northeast, with support mainly from the public sector, and little integration with industrial tree growers.

The situation is understandable and perhaps economically realistic, if not ideal from the viewpoint of ambitious tree breeders. There are some favorable signs of greater cooperation. If these materialize into a serious commitment by industries and public agencies to intensive tree growing, particularly artificial regeneration, then adequate support for more comprehensive tree improvement programs can be expected. When that occurs, the accumulated genetic knowledge and selected trees can be utilized more effectively.

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